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PHYTOPLANKTON BIOMASS AND PRODUCTIVITY IN THE WESTERN ANTARCTIC PENINSULA REGION

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The Palmer Long-Term Ecological Research (LTER) area, the area west of the Antarctic Peninsula, is an important component of the Antarctic marine ecosystem which is composed of a coastal and continental shelf zone (CCSZ) annually swept by the marginal ice zone (MIZ). This coastal component of the Antarctic marine ecosystem is influenced by meltwater from glaciers and icebergs, inclusive of areas providing some protection from wind and storms, potentially enriched by essential micronutrients from land, supportive of massive blooms that do, in fact, reduce macronutrients and supportive of relatively high levels of primary productivity. We present an overview of the temporal and spatial variability in phytoplankton biomass and primary productivity for the LTER area based on ship and satellite data collected in this region and summarize factors controlling primary productivity. If historical data are representative, considering the complex space/time variability of the area, then the average primary productivity of this region is of the order of a few hundred gC m^{-2} y^{-1} which, while about a factor of 5 lower, is roughly comparable to other productive coastal areas of the world's oceans.

1. INTRODUCTION

Waters of the Southern Ocean are characterized by a pronounced seasonal variability in incoming solar radiation, low temperatures, high inorganic nutrients, as well as the presence, formation, and melting of sea ice. The Antarctic marine ecosystem, which is composed of an interconnected system of hydrographic and biogeochemical sub-divisions [*Treguer and Jacques*, 1992], includes open ocean, frontal regions, shelf-slope waters, sea ice and marginal ice zones. This ecosystem is bounded on the north by the Polar Front and the south by the Antarctic continent and is among the largest readily defined ecosystems on Earth (36×10^6 km^2) [*Hedgpeth,* 1977; *Young,* 1991]. Oceanic and atmospheric processes and biogeochemical fluxes within this system are globally significant, sensitive to perturbation and poorly understood relative to more accessible marine ecosystems [*Harris and Stonehouse,* 1991; *Johannessen et al*., 1994]. Trophic relationships within this system are complex, yet often with few trophic links separating phytoplankton from top predators, and this ecosystem is an environment high in macronutrients relative to other large ocean environments [*Llano,* 1977; *Smith,* 1990]. We do not yet have an adequate understanding of the chemical, optical, physical and biological processes regulating primary production and the subsequent carbon fluxes within this ecosystem, nor do we yet understand fully the fundamental similarities and differences between this important marine system and those in more temperate latitudes. Indeed, understanding processes regulating this high nutrient, low plankton biomass environment is a key outstanding problem. Here we review factors controlling phytoplankton growth and accumulation in waters of the Southern Ocean, gather pigment biomass and phytoplankton productivity data from the western Antarctic Peninsula region, and summarize general characteristics of this marine ecosystem based upon historical data (Figure 1).

Most investigators of the Southern Ocean, from the first explorers up to the 1970s, believed that the Southern Ocean was a rich ecosystem with high levels of primary production [*Jacques,* 1989]. Now, with the advent of more comprehensive sampling, it is generally believed that primary production in the Antarctic is low, even though nutrient levels are high [*El-Sayed,* 1978; *Jacques,* 1989; *Priddle et al*., 1986a; *Holm-Hansen and Mitchell,* 1991]. This opinion may again come under question with the advent of satellite technology and increased spatial/temporal sampling since accurate estimates of large scale phytoplankton distributions, both spatially and temporally, are difficult to obtain with traditional shipboard measurements. This is particularly true in light of the inaccessibility of the Southern Ocean during much of the year. Imagery from the Coastal Zone Color Scanner (CZCS) was used recently by *Sullivan et al.* [1993] and *Comiso et al.* [1993] to investigate the distributions of phytoplankton blooms in the Southern Ocean, and by *Arrigo and McClain* [1994] to analyze blooms of phytoplankton in the western Ross Sea. Using this approach, they concluded that the spring-to-summer primary productivity was three to four times the values previously reported for this region. Thus, the detection and mapping of phytoplankton blooms are crucial to estimating the

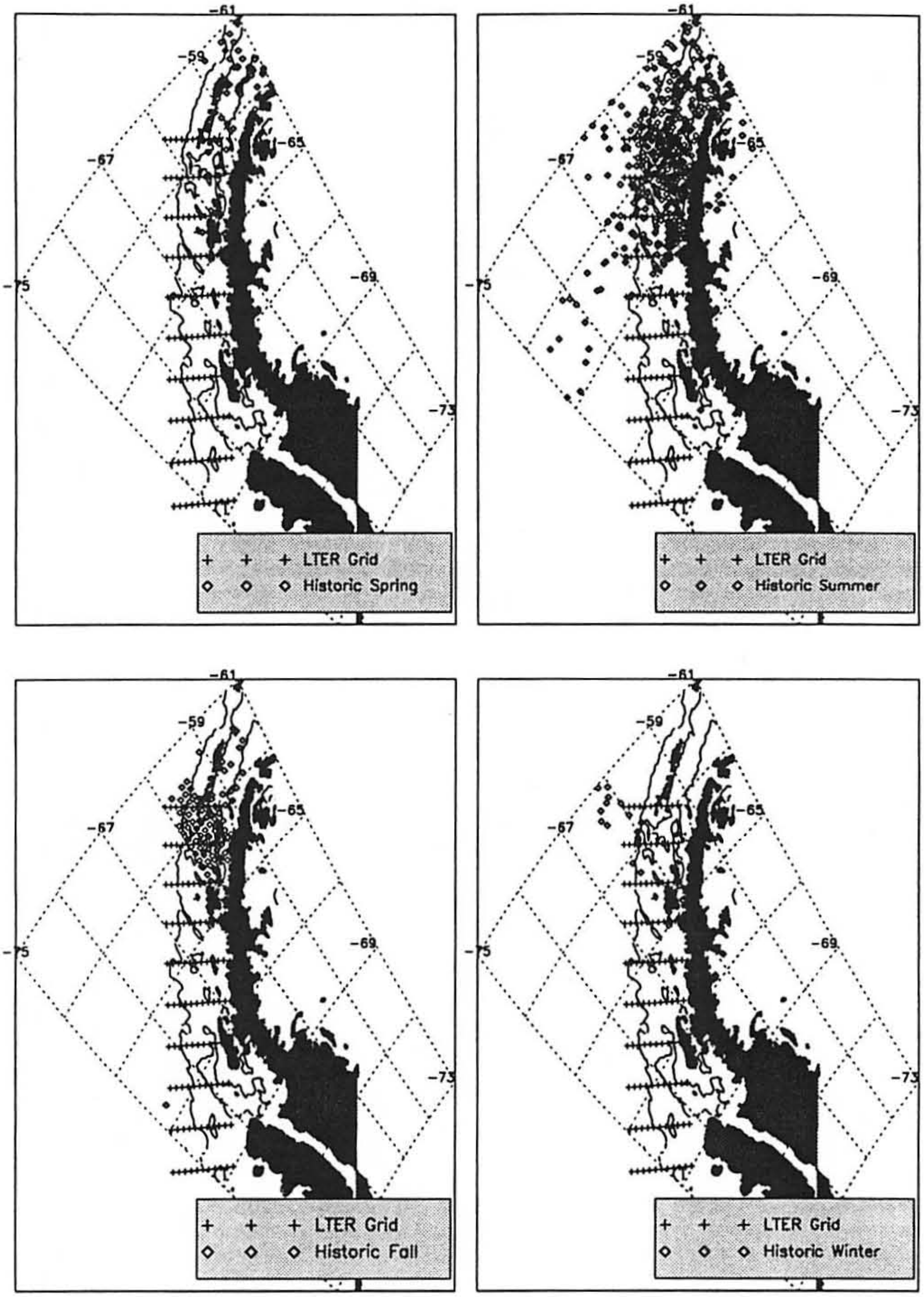

Fig. 1. Seasonal distributions of station locations (diamonds) for historical chl-a and productivity data (listed in Tables 1 and 2) in the Palmer LTER region west of the Antarctic Peninsula (shown in stereographic projection). The latitude-longitude grid (light lines) is from 61-73°S latitude and from 65-75°W longitude. Cardinal stations comprising the LTER large scale sampling grid are indicated by +'s. Seasons are defined as: spring (Sept, Oct, Nov), summer (Dec, Jan, Feb), fall (Mar, Apr, May) and winter (June, July, Aug). The thin solid line shows the 500 m bottom contour, an indicator of the shelf break.

total productivity of remote regional areas, such as the Palmer LTER area west of the Antarctic Peninsula.

Sea ice is a distinguishing characteristic of the Antarctic marine ecosystem, and its spatial and temporal variability is expected to affect all trophic levels, both directly and indirectly. In particular, sea ice modulates and may often be a major factor regulating the timing and magnitude of seasonal phytoplankton productivity in the Southern Ocean. The marginal ice zone (MIZ) can be viewed as an oceanographic front which often supports high biological productivity. Factors (e.g., temperature, light, nutrients) and processes (e.g., water column stability, grazing, sinking, advection) which regulate primary production in temperate waters are themselves often linked to, or modulated by, the presence or absence of sea ice in these waters. Further, sea ice may act as a repository or an inoculum for algae, storing remains of a fall bloom for release the following spring [*Garrison et al.*, 1986].

Low temperatures are known to reduce metabolic processes, may effect the efficiency of nutrient utilization [*Tilzer et al.*, 1986] and have long been thought to depress phytoplankton growth [*Saijo and Kawasha*, 1964]. However, understanding of the overall influence of low temperatures on the marine ecosystem remains problematic, and the response of the system, for example to possible warming, may be more influenced by indirect effects (e.g., sea ice, water column stability) than temperature *per se*.

Seasonal variability in photosynthetically available radiation (PAR) clearly plays a primary role in the control of primary productivity on a seasonal basis, with nearly continuous darkness in winter alternating with continuous light in summer. For open ocean areas, Sverdrup's hypothesis linking depth of the euphotic zone, the mixed layer depth, photosynthesis and respiration to a critical depth below which productivity cannot be sustained has been invoked as an important mechanism limiting standing stock [*Mitchell and Holm-Hansen*, 1991b; *Nelson and Smith*, 1991]. However, use of the concept of critical depth in Antarctic waters remains controversial [*Priddle et al.*, 1986b] and has recently been reviewed [*Platt et al.*, 1994]. Phytoplankton blooms within the MIZ are hypothesized to play a significant role in the overall productivity of the Southern Ocean. Melting ice induces water column stability which concentrates and restricts algal blooms to the well illuminated upper layer [*Smith and Nelson*, 1986; *Wilson et al.*, 1986; *Nelson et al.*, 1987]. In contrast, PAR under extensive ice cover is relatively low and significantly limits photosynthesis and growth.

Macronutrients (nitrate, silicic acid, and phosphate) are usually plentiful, except in some coastal inlets and are not considered to be a key factor limiting phytoplankton productivity. The role of micronutrients, for example iron, is controversial, and we are far from understanding the role, if any, of trace nutrients in the Southern Ocean [*Buma et al.*, 1991; *de Baar et al.*, 1995]. Further, the potential roles of heterotrophic microorganisms, both open ocean and those associated with sea ice communities, are poorly known. Grazing by microzooplankton has also been suggested as a mechanism for maintaining low plant biomass and consequently low nutrient uptake [*Miller et al.*, 1991; *Frost*, 1991; *Mitchell and Holm-Hansen*, 1991a]. Again, relatively little is known to either support or refute this hypothesis. As a consequence of these uncertainties, potentially significant elements of trophic organization associated with phytoplankton productivity are currently unknown.

The Palmer LTER area, the area west of the Antarctic Peninsula, is a complex combination of two distinctive functional sub-divisions of the Antarctic marine ecosystem [*Treguer and Jacques*, 1992]. It is a coastal and continental shelf zone (CCSZ) and is a part of the seasonal sea ice zone (SIZ) swept by the yearly retreat of sea ice. It is a complex area where typical on/offshore gradients in bottom topography and in the physical, optical, chemical and biological water column characteristics are modulated alongshore by the advance and retreat of sea ice. Here we refer to this component of the Antarctic marine ecosystem as the west Antarctic Peninsula coastal ecosystem, or coastal ecosystem for short. In addition to enhanced productivity associated with the MIZ, there is evidence that large phytoplankton blooms are a consistent and geographically significant component of primary productivity within this coastal ecosystem [*Holm-Hansen et al.*, 1989]. Consequently, this coastal ecosystem is higher in phytoplankton biomass and productivity and likely combines a more complex mix of controlling processes than more pelagic areas of the Antarctic marine ecosystem. Compared with other areas of the world's oceans, there are relatively few phytoplankton biomass and productivity data for the Southern Ocean. Within the Palmer LTER area, most historical data are concentrated in the northern area of the Peninsula. We present an overview of the temporal and spatial variability in phytoplankton biomass (measured as chlorophyll-a) and primary productivity for the LTER area based on data collected in this region during the past 30 years (1960-1990) of Antarctic research. We also summarize major factors which are thought to regulate the abundance and distribution of phytoplankton in the Southern Ocean and discuss the possible contributions of these factors to the observed patterns.

2. PRIMARY PRODUCTIVITY CONTROLS

Primary production in the Southern Ocean may be regulated by a number of factors. Regulation can occur either by factors that control cell growth rates (temperature, light, and nutrients) and/or by those that control the accumulation rate of cells in the euphotic zone and hence population growth (grazing, water column stability, and sinking). These factors are not mutually exclusive and all or a combination of these factors may regulate primary production in different areas of the Southern Ocean.

2.1. Temperature

The question arises whether phytoplankton of the Antarctic have adequately adapted to the cold temperatures of their environment. Phytoplankton communities at the ice edge are exposed to temperatures as low as -1.8°C and near surface waters of the open ocean are typically between -1.8 and 3°C [*Jacques*, 1989]. In general, metabolic processes (e.g., enzymatic reactions involved in carbon fixation) are slower with lower temperatures and efficient utilization of nutrients may be impossible [*Tilzer et al.*, 1986].

The effects of temperature on primary production have been investigated for several Antarctic marine phytoplankton. In the western Scotia Sea and Bransfield Strait, *Neori and Holm-Hansen* [1982] found that photosynthetic rates increased between 4.5 and 7°C and rates decreased above 7-8°C. They conclude that in Antarctic surface water during the austral summer, the rate of photosynthesis was limited by thermodynamic effects on metabolic reactions. Similarly, *Tilzer et al.* [1986] found that at the low temperatures occurring in the Scotia Sea and Bransfield Strait region both light-saturated and light-limited photosynthesis were temperature-dependent. This was attributed to a temperature dependence of maximum quantum yields [*Tilzer et al.*, 1986; *Tilzer and Dubinsky*, 1987]. Both photosynthetic capacity (photosynthesis per unit chlorophyll biomass at optimum irradiance) and maximum quantum yield were, on average, lower in Antarctic phytoplankton than for populations from more temperate latitudes. These researchers also measured photosynthesis and respiratory losses for Antarctic phytoplankton and found that the Q_{10} value for photosynthesis is lower (1.4 - 2.2) than for respiration (2.3 - 12). They suggest that under nutrient-replete and near zero temperature conditions of the Southern Ocean this differential temperature dependence is a key factor in controlling phytoplankton productivity by maintaining a more positive biomass balance than would be anticipated in warmer waters. This lower respiration during winter minimizes metabolic costs and enhances survival of an inoculum to initiate a population build-up in spring. *Tilzer et al.* [1986] also conclude that Antarctic marine phytoplankton have not evolved mechanisms to overcome the inhibitory effects of low temperature on photosynthesis, although the temperature optimum for photosynthesis was low by comparison with phytoplankton from lower latitudes.

More recently, *Wiencke et al.* [1993] studied the photosynthetic performance of macroalgae from Antarctica in the laboratory. They determined that the brown and red algal species exhibited higher rates of maximal photosynthesis (P^B_{max}) at 0°C than Arctic species measured at similar temperatures. Moreover, temperature optima for photosynthesis were lower in several Antarctic species than in temperate and Arctic species. Optimum temperatures for photosynthesis in their experiments ranged from 5 to 20°C depending on the species, which is generally higher than ambient temperatures in the Antarctic. Additionally, the photosynthesis to respiration ratios (P:R) strongly decreased with increasing temperatures. Based on these results, *Wiencke et al.* [1993] conclude that the algae have undergone considerable physiological adaptation to the prevailing low temperature conditions of the Antarctic, but may not be at their optima for production.

However, other evidence suggests that temperature optima for growth or increased biomass may be relatively close to ambient temperatures [*Priddle et al.*, 1986b]. Also, *Uno* [1983] found that maximal chl-**a** concentrations occurred within the temperature range of -1.4 to -0.3°C in the Indian Ocean. Further, the presence of massive phytoplankton blooms clearly demonstrates that rapid growth is possible at ambient temperatures, and the relative constancy of temperature in Antarctic waters cannot account for the spatial variability seen in phytoplankton biomass or production at all scales of observation [*Bidigare et al.*, 1988]. Thus, while temperature seems to exert some pressure, and may in fact set an upper limit for specific growth of phytoplankton, the presence of areas with very high biomass in the Southern Ocean indicates that low temperatures are not a dominant limiting factor for the population growth of phytoplankton.

2.2. Light

The Antarctic ecosystem is subject to large variations in incident radiation. The amount and quality of light utilized by Antarctic phytoplankton is dependent on several factors: (1) seasonal variations in incident radiation, (2) diel variations in incident radiation, (3) atmospheric conditions (e.g., clouds), (4) transmission across the air/sea interface which can be ice and snow covered, (5) optical properties of the water, (6) movements of algae within the water column, and (7) light harvesting capabilities of algae. All these factors lead to high variability in the irradiance regime and thereby effect the growth rate of phytoplankton. However, phytoplankton respond to variable irradiance by photoadaptive processes, including alteration of the photosynthetic apparatus of the cells and shifts in the carbon to chlorophyll ratio (C/chl-**a**), which works to minimize the impact of variable irradiance on growth rates [*Sakshaug and Holm-Hansen*, 1986].

To the extent that regional productivity is controlled by physical factors (e.g., temperature and light), it is generally expected that photosynthesis vs. irradiance (P-I) parameters should reflect characteristics of the environment. Reviews have shown that different communities of polar phytoplankton exhibit considerable variation in photosynthetic parameters, and some general conclusions have begun to emerge [*Harrison and Platt*, 1986; *Smith and Sakshaug*, 1990].

Investigations indicate that most Antarctic phytoplankton are adapted to handle low light conditions and are considered to be shade-adapted. In other words, the light intensity needed to saturate photosynthesis (I_k) has been found to be lower in Antarctic regions than for low latitude regions [*Jacques*, 1983; *Sakshaug and Holm-Hansen*, 1986; *Tilzer et al.*, 1986; *Cabrera and Montecino*, 1990; *Wiencke et al.*, 1993; *Figueiras et al.*, 1994]. Lower values for the maximum photosynthetic rate (P^B_{max}) for polar phytoplankton are generally attributed to low temperatures. The initial slope of the P-I curve (α) for low-light-adapted phytoplankton is, on average, slightly lower than high-light-adapted phytoplankton from lower latitudes. The photoinhibition parameter (β) is higher in low-light-adapted phytoplankton with the expectation of increased susceptibility to inhibition.

Tilzer et al. [1985] concluded that due to reductions in photosynthetic capacity and lower light-limited quantum yields, phytoplankton in Antarctic waters utilize incident light inefficiently, even in situations where biomass accumulation is high. They argue that the low water temperatures are responsible for this reduction in utilization efficiency of incident radiation. Others [*Figueiras et al.*, 1994; *Helbling et al.*, 1995] determined that I_k values for phytoplankton correspond to the mean light available in the mixed water column and suggest that Antarctic phytoplankton are adapted to take maximum advantage of the light available in a rapidly mixed water column where nutrients are not limiting. Both incident surface irradiance and the average irradiance within a deeply mixed water column are relatively low, so these results illustrate the important influence exerted by the environment from which the phytoplankton were collected. *Sakshaug and Holm-Hansen* [1986] also state that "the most extreme photoadaptational flexibility may be found in ice-edge communities." Given the vastly differing light regimes that ice-edge communities experience (e.g., fully shaded under the ice vs. complete surface illumination), this photoadaptive flexibility is not surprising. The above observations are relevant for non-winter periods. The winter period, with short days and low light levels, has been shown to have low productivity and to add a relatively minor contribution to yearly production [*Brightman and Smith*, 1989].

Water column stability (see below) and the in-water light regime establish the relative magnitudes and time scales of mixing and photoadaptation of phytoplankton [*Lewis et al.*, 1984]. Within the context of these time scales, the layer in which there is a net gain of photosynthesis (i.e., photosynthesis exceeds respiration) is considered to be the euphotic zone. The depth of the euphotic zone is conventionally considered to be the depth to which 1% of the surface radiation penetrates. In early work, *Burkholder and Mandelli* [1965] determined that more than half of the chl-a content was below the euphotic zone. Similarly, in the Ross Sea, *El-Sayed et al.* [1983] found that more than 25% of the water column productivity occurred below the euphotic zone and concluded that Antarctic phytoplankton are capable of net photosynthesis at depths significantly below the conventional 1% light depth. *Bodungen et al.* [1986] considers the euphotic zone to extend to the 0.1% light level and shows several profiles of carbon assimilation rates (mg C (mg chl-a)$^{-1}$ h^{-1}) that remain fairly constant from the 1% to the 0.1% light level. Similarly, *Weber and El-Sayed* [1987] reported several stations in the Bransfield Strait where primary productivity did not drop off until well below the 1% light level. These data suggest that there likely is photosynthesis occurring below the 1% light level, but results to date have not included complete consideration of time scales of mixing and photoadaptation and the significance of viable phytoplankton at depths below the 1% light level remains unknown.

In addition to light used in photosynthesis (primarily in the visible region of the spectrum), radiation in the ultraviolet region may also play a role in Southern Ocean primary production. There is considerable evidence that ultraviolet radiation (UV) can cause biological damage at the molecular, cellular, population and community levels [*Smith and Cullen*, 1995; *Hader et al.*, 1995]. The springtime stratospheric ozone layer over the Antarctic is thinning (the proverbial 'ozone hole') and results in increased midultraviolet (UVB, 280-320 nm) radiation reaching the surface of the Southern Ocean [*Smith et al.*, 1992a]. *Smith et al.* [1992a], during a 6-week cruise in the marginal ice zone of the Bellingshausen Sea, conclusively measured a UV-B impact on Antarctic phytoplankton communities located under the ozone hole. While the ecological significance and magnitude of this impact continue to be debated, the fact remains that the Southern Ocean is currently experiencing enhanced levels of UVB, with a measurable impact on Southern Ocean phytoplankton productivity.

High variability in the irradiance regime is reflected in considerable variation in photosynthetic parameters and indicate that observed P-I values represent one extreme of an environmental continuum. Daylength, because of its wider range, appears to have a more pronounced effect on high-latitude algal growth rates [*Gilstad*, 1987] than for low-latitude communities. In addition, ice and snow cover are highly attenuating and greatly reduce the magnitude and increase the variability of available PAR. The question of water column mixing is critical to a description of the in-water irradiance regime, and physical factors (e.g., sea ice, wind) regulate both the PAR available at depth and time scales at which phytoplankton experience the variable light regime. Thus, even though Antarctic phytoplankton have adapted to low light conditions, their use of light may strongly depend on the marine habitat and the corresponding light history in which the plankton are found.

2.3. Nutrients

In general, the pools of macronutrients (phosphate, nitrate, and silicate) in Antarctic waters are observed to be far in excess of phytoplankton needs and are, therefore, not believed to limit phytoplankton growth [*Bidigare et al.*, 1988; *Jacques*, 1989; *Martin et al.*, 1990]. However, there may be mesoscale areas of significant macronutrient depletion. *Holm-Hansen et al.* [1989], studying phytoplankton blooms in the vicinity of Palmer Station, presented clear evidence that massive coastal area blooms may lower nutrient concentrations to such a degree that one or more nutrients may be limiting with respect to growth rates. This work has important implications since they also suggest that large blooms seem to be characteristic of the coastal ecosystem both on a yearly basis and over significant geographic areas. *Nelson and Treguer* [1992] recently reported an intense, diatom-dominated, ice-edge phytoplankton bloom in the southwestern Ross Sea that resulted in depletion of silicic acid, nitrate, and phosphate to unusually low concentrations. They argue that silica limitation may limit diatom growth in these situations. However, they report that significant silica limitation in open ocean areas of the Southern Ocean is not likely, given the observed affinity for silicic acid [*Nelson and Treguer*, 1992].

Considerable effort has been devoted to testing the potential role of micronutrients (vitamins and trace metals) in limiting Antarctic biomass and production. The low concentrations of vitamin B_{12} and thiamin may play a limiting role in phytoplankton growth or in controlling the species composition [*Bidigare et al.*, 1988; *Jacques*, 1989]. *Hayes et al.* [1984] carried out enrichment experiments using macronutrients iron, copper, zinc, manganese and a vitamin mixture and found no significant increase in carbon fixation or phytoplankton growth. *Jacques et al.* [1984] carried out enrichment experiments using zinc, molybdenum, cobalt, manganese, and iron and showed that these trace metals do not limit primary production. However, with the advent of trace-metal clean techniques, these results have been questioned and new interest in the role of trace metals limitation, particularly iron, has been aroused [*Martin et al.*, 1990].

The primary input of iron to the oceans occurs via aeolian dust blown onto the surface. Consequently, open ocean iron concentrations in surface waters generally exist at picomolar levels and may not be sufficient to support maximum phytoplankton production and growth. Using trace-metal clean techniques, addition of iron to seawater samples of high nutrient, low chlorophyll waters has been shown to stimulate the growth of phytoplankton, especially diatoms [*Martin et al.*, 1990;

de Baar et al., 1990]. It is important to note that iron did not stimulate growth in all of the experimental samples under analysis. Furthermore, in several of these experiments, phytoplankton growth was also observed in control samples that were not subject to iron enrichment [*de Baar et al.*, 1990; *Banse*, 1991; *Buma et al.*, 1991].

How one extrapolates these types of shipboard and laboratory experiments to whole ecosystems is an important question. *Brandini* [1993] studied phytoplankton biomass accumulation in a stable water column in Admiralty Bay (King George Island) that had non-limiting iron concentrations. He found that the grazing pressure precluded phytoplankton biomass accumulation, even though the light/nutrient regime was optimum. In another study, *Holm-Hansen et al.* [1994] recently hypothesized based on circumstantial evidence, that the deep surface chl-**a** maxima (50-100 m depth) consistently found in a certain region of the Antarctic waters around Elephant Island are indicative of a micronutrient limitation, such as iron.

A comprehensive *in situ* experiment on iron limitation of phytoplankton in high nutrient, low chlorophyll waters was conducted by enriching a 64 km^2 area in the open equatorial Pacific [*Martin et al.*, 1994]. After the iron enrichment, *Martin et al.* [1994] detected a doubling of plant biomass, a threefold increase in chlorophyll, and a fourfold increase in plant production. In addition, *Kolber et al.* [1994] used a sensitive fluorescence method and found an increase in the quantum efficiency of photosystem II (PSII) and cellular chlorophyll in all phytoplankton size classes in response to this iron enrichment. While the experiment showed an apparent short-term biological response to iron enrichment, the effect of the enrichment was small relative to the biogeochemical effect that could have been achieved if all the major nutrients were consumed. More recently, a similar iron enrichment experiment was completed in June 1995 in the same area of the Pacific Ocean. In this experiment, instead on one large addition of iron, iron was added in three smaller doses. Preliminary results indicate a dramatic 30- to 40-fold increase in chlorophyll and absorption of 350,000 kg of carbon dioxide from the seawater as a result of the iron enrichment [*Monastersky*, 1995]. Unlike the earlier experiment where a front of low-salinity water forced the iron enriched water to sink, the treated water in this latest enrichment experiment stayed at the surface throughout the experiment making the iron more available to phytoplankton. These results provide evidence that iron could control the rate of phytoplankton growth in parts of the ocean. How this translates to the HNLC waters of the Southern Ocean remains an outstanding question. Conclusions drawn from the use of models [*Peng and Broecker*, 1991a; *Peng and Broecker*, 1991b; *Mitchell and Holm-Hansen*, 1991b] suggest that massive iron additions to the Southern Ocean would fail to significantly sequester CO_2 without an additional mechanism for increasing stratification of the upper layers, thus indicating the synergistic interaction of factors limiting phytoplankton growth. The issue of iron limitation continues to be debated [*de Baar et al.*, 1995; *Wells et al.*, 1995].

2.4. Grazing

Grazing is known to affect phytoplankton growth and distribution in a number of ways. An inverse relationship is often noted between phytoplankton biomass and zooplankton, particularly krill populations [*Bidigare et al.*, 1986; *Bidigare et al.*, 1988; *Jacques*, 1989; *Ross and Quetin*, 1991]. Obviously, intense grazing by krill can limit the growth of phytoplankton populations. In an experimental mesocosm, *Price* [1989] demonstrated that krill density grew by an order of magnitude within only 1/2 hour of a phytoplankton bloom and argues that krill have the ability to detect and remain within a phytoplankton patch. This suggests that predator-prey cycles can be rapid in the Southern Ocean and grazing from predators could serve to limit phytoplankton populations.

The amount of grazing may be indicated by the concentrations of phaeopigment relative to chl-**a**. Zooplankton grazing is the dominant source of phaeophorbide-**a**, which is formed during the sequential breakdown of chl-**a** during zooplankton digestion [*Bidigare et al.*, 1986]. Based on the concentrations of phaeophorbide-**a**, researchers have concluded that phytoplankton abundance in parts of the Southern Ocean can be physically controlled and modified by zooplankton grazing activity [*Bidigare et al.*, 1986; *Jacques and Panouse*, 1991].

Not only can grazing influence hourly and daily variability in phytoplankton, it can also effect seasonal variations in phytoplankton. *Priddle et al.* [1986b] discuss an instance when the standing stock of krill in the winter around South Georgia was much lower than expected, while phytoplankton concentrations were higher than expected. Without the typically high krill populations, the phytoplankton concentrations were not diminished to their normal low levels expected at this time. The normal winter decline of phytoplankton may be attributed to zooplankton grazing effects exceeding phytoplankton replenishment by growth. On a similar seasonal time scale, *Minas and Minas* [1992] conclude from their net community production analysis of the Antarctic that if both the grazing and iron hypotheses are valid in the Antarctic Ocean, the iron limitation starts late, when most of the yearly photosynthesis period is over. Additionally, *Jacques and Panouse* [1991] hypothesize that a grazing induced seasonal cycle in the Weddell/Scotia system during early summer changes from a new production based ecosystem towards a regenerated system and progresses from north to south, partially associated with the retreat of the pack ice. In addition to both daily and seasonal time scales, the effects of grazing on phytoplankton biomass and production have not been explored on interannual and longer time scales.

Grazing may influence also the species composition and size distribution of phytoplankton. *Weber and El-Sayed* [1987] report that the Southern Ocean phytoplankton community is largely dominated by nanoplankton (cells $< 20\ \mu m$) and picoplankton cells ($< 1\ \mu m$). They find, in the Drake Passage/Bransfield Strait region, that the integrated water column chl-**a** was 39-98% nanoplankton and 5-74% picoplankton. *Villafane et al.* [1993] found near Elephant Island only 30-50% nanoplankton and 50-70% microplankton. However, this preponderance of small sized plankton may not accurately reflect the active phytoplankton population in the Southern Ocean. *Gieskes and Elbrachter* [1986] demonstrated that a large portion of the chlorophyll measured in the nanoplankton size fraction is due to the presence of free-floating, extracellular chloroplasts that have been released from the cells by turbulent storms or by grazing. Reportedly, at low temperatures prevailing in Antarctic waters, these free-floating chloroplasts remain fluorescent and may even be able to take up ^{14}C for several days. The fragility of cells in old phytoplankton populations, and thus the propensity to cause free-floating chloroplasts, is greater than in populations that are growing actively and are in good physiological condition. Such reasoning may explain the instances when low nanoplankton concentrations are found in regions where chlorophyll concentrations are high (new populations) and vice versa.

Heavy selective grazing on phytoplankton by various types of zooplankton (protozoans, copepods, salps, krill) could also lead to an actual shift in species composition and a significant reduction in the biomass of larger, bloom-forming phytoplankton. *Jacques and Panouse* [1991] demonstrate that the high nanoplankton concentrations found in the marginal ice zone consist of active, small diatoms, prymnesiophytes and cryptophycean and were not the product of chloroplast particles. They conclude that the high proportion of nanoplankton may have arisen due to grazing pressure by krill on large cells. Moreover, shipboard grazing experiments have shown that different size fractions of krill consume all particles with the same efficiency except the nanoplankter cryptophycean, which are often the only phytoplankton left at the end of the experiment [*Jacques and Panouse*, 1991]. Thus, grazing may play a role in determining the size structure of the phytoplankton in the Southern Ocean.

2.5. Water Column Stability

There is considerable evidence to suggest that stability of the water column plays a crucial role in controlling primary production in the Southern Ocean. With vertical mixing of the water column, phytoplankton may not be allowed to remain in a favorable light regime for photosynthesis. This is especially true for the Antarctic system which is characterized by high winds and often deep, well mixed waters. As early as the 1930s, *Hart* [1934] considered water column stability to be the controlling factor for phytoplankton biomass buildup and speculated that zooplankton grazing was the most likely reason for its decline thereafter. *Bidigare et al.* [1986] found the highest pigment concentrations in stratified waters where vertical stability was enhanced. In their evaluation of the extensive BIOMASS dataset, *Priddle et al.* [1994] observed that very unstable water columns had low biomass, and that very high biomass only occurred in stable water columns.

Several researchers have utilized mathematical models in an attempt to evaluate the sensitivity of bloom formation and water column stability. *Sakshaug et al.* [1991] used a one-dimensional ecosystem model to determine that periodic deep mixing caused by strong winds may severely retard the development of blooms before macronutrients have been exhausted. Moreover, even modeling with moderate mixing depths (40-50 m) and moderate loss rates, bloom development was prevented during the brightest time of year. Using a similar approach, *Mitchell and Holm-Hansen* [1991b] concluded that phytoplankton bloom development is dependent upon the factors that control vertical mixing and phytoplankton loss rate.

The vertical stability generated by meltwater during the retreat of the MIZ have been hypothesized to cause ice-edge blooms [*Gran*, 1931; *Marshall*, 1957; *Smith and Nelson*, 1986; *Smith et al.*, 1987]. Observations and modeling of the MIZ in the Weddell Sea showed that the initiation of the phytoplankton bloom was determined by physical processes operating in the MIZ at the time of ice melting [*Lancelot et al.*, 1993]. The duration, strength and frequency of wind mixing events determined both the distance of the phytoplankton bloom from the ice edge and the occurrence of secondary phytoplankton blooms in the ice-free area during the summer period. The magnitude and extent of ice edge blooms is thus determined by the combined action of meltwater stability and meteorological conditions.

3. PHYTOPLANKTON BIOMASS AND PRODUCTION WEST OF THE ANTARCTIC PENINSULA

3.1. Historical Data

There are relatively few *in situ* observations of chl-**a** concentration and primary production west of the Antarctic Peninsula (Tables 1 and 2). Historical data for this region of the Southern Ocean are strongly biased by season, with most observations in spring and summer and virtually none in winter, as well as by location, with most data from the northern portion of the region in the vicinity of the South Shetland Islands (Figure 1). Thus, annual estimates based on these determinations will be biased by the summer weighted sampling distribution and lack of data from the southern end of the peninsula. Although low irradiance and low chl-**a** concentration during winter months will not greatly affect overall estimates, the contribution of spring and fall blooms associated with the MIZ, fronts or topography might be larger than what has been observed to date.

Historical chl-**a** and productivity data based on shipboard observations for this region of the Southern Ocean (Tables 1 and 2) were obtained from a variety of sources including a literature review using the Cold Regions Database-Antarctic Bibliography, which provided citations on papers from the 1960's up through 1990. When published chl-**a** and productivity data were presented only as figures (vertical profiles) and/or contours, the graphs were scanned, and data retrieval software was used to approximate numerical values from the graphs. We also used the BIOMASS dataset [*Thorley and Trathan*, 1994] which was compiled from three different international field experiments in the Southern Ocean. The BIOMASS chlorophyll measurements were obtained from 1980 to 1985 primarily from late spring (October) through early fall (May) with the preponderance of data during summer (December - February). Chlorophyll data were also obtained from the RACER program conducted in the southwestern Bransfield Strait region between December and March 1987. Additionally, we obtained historical chlorophyll data from NASA/Goddard Space Flight Center SeaWiFS Project - Calibration/Validation group. For all of the above sources of historical data the fluorometric method [*Strickland and Parsons*, 1968] was commonly used for determination of chlorophyll concentrations, but technical details varied. Appearance of internal consistency was the only quality control we applied when compiling these data.

TABLE 1. Historical chlorophyll data within the Palmer LTER region

Source	Date	No. Sta.	Depth (m)	Latitude (deg S)	Longitude (deg W)	Chl-a ($mg\ m^{-3}$)	Integrated[d] Chl-a ($mg\ m^{-2}$)
Burkholder and Sieburth [1961]	12/58 - 1/59	38	0 - 100	35 - 65	56 - 64	0.10 - 27	*164 - 308*
El-Sayed et al. [1964]	3/63	15	0 - 50	55 - 64	58 - 66	0.14 - 5.9	*7 - 279*
Mandelli and Burkholder [1966]	2/65	35	0 - 50	61 - 65	57 - 66	0.20 - 23	20 - 209
Burkholder and Mandelli [1965]	3/65	8	0 - 100	62 - 68	57 - 78	<0.01 - 27	6 - 202
Bienati et al. [1971]	3/70 - 1/71	1	0 - 90	65 - 65	63 - 63	<0.01 - 30	*12 - 89*
Krebs [1974]	6/72 - 12/73	1	3	65 - 65	64 - 64	0.23 - 27	-
Bienati et al. [1977]	12/72 - 2/73	1	0 - 15	65 - 65	63 - 63	0.34 - 36	154 - 265
NASA data (japan)[c]	12/74 - 12/85	55	0	60 65	55 85	0.06 - 1.7	-
Hapter and Wozniak [1983]	12/77 - 3/78	1	1 - 50	62 - 62	59 - 59	0.21 - 6.6	*27 - 170*
Hayes et al. [1984]	1/79 - 1/79	4	0	57 - 69	40 - 69	0.25 - 2.5	-
Schneider [1983]	12/80 - 2/81	44	0 - 100	55 - 64	50 - 64	<0.01 - 10	*19 - 385*
Tilzer et al. [1985]	11/80 - 12/80	23	0 - 100	55 - 64	54 - 64	0.48 - 10	*27 - 170*
Bolter and Dawson [1982]	11/80	14	0 - 1000	62 - 64	55 - 64	0.10 - 10	*151 - 428*
Bodungen et al. [1986]	11/80	82	0 - 100	62 - 63	55 - 58	0.24 - 12	49 - 209
Schnack et al. [1985]	12/80	3	0 - 100	61 - 63	55 - 62	0.12 - 3.8	44 - 200
Dawson et al. [1985]	1/81	12	1	62 - 62	58 - 58	0.50 - 13	-
Ronner et al. [1983]	1/81	13	5 - 75	52 - 61	33 - 50	0.10 - 2.2	-
Uribe [1982] (ITFX)[a]	1/81 - 2/81	40	0 - 50	61 - 64	54 - 63	0.11 - 8.8	*14 - 335*
Lipski [1982] (SIFX)[a]	2/81 - 3/81	42	0 - 200	60 - 65	56 - 66	<0.01 - 4.4	*3 - 200*
Tokarczyk [1986]	3/81 - 2/82	9	0 - 300	62 - 62	58 - 59	0.10 - 1.6	46 - 205[e]
Sakshaug and Holm-Hansen [1986]	3/81 - 2/83	7	5 - 100	60 - 68	47 - 77	0.13 - 2.3	-
Teixeira et al. [1986]	1/83 - 2/83	48	0 - 200	61 - 65	53 - 65	0.10 - 2.4	7 - 39
Tilzer et al. [1986]	10/83 - 11/83	16	0 - 5	60 - 63	54 - 61	0.19 - 0.8	-
Gieskes and Elbrachter [1986]	11/83	50	5	60 - 64	54 - 61	0.08 - 0.8	-
Bodungen [1986]	11/83 - 12/83	64	0 - 300	53 - 64	55 - 63	0.07 - 15	28 - 234[f]
Lipski [1985] (SIS1)[a]	12/83 - 1/84	56	0 - 150	60 - 65	51 - 66	0.05 - 11	*6 - 446*
unpub. (BES1)[a]	1/84 - 2/84	43	0 - 150	60 - 64	54 - 67	<0.01 - 1.7	*1 - 21*

TABLE 1. (continued)

Source	Date	No. Sta.	Depth (m)	Latitude (deg S)	Longitude (deg W)	Chl-a (mg m^{-3})	Integrated[d] Chl-a (mg m^{-2})
Uribe [1987] (ACS1)[a]	1/84 - 2/84	47	0 - 100	62 - 65	54 - 66	0.02 - 8.1	*2 - 251*
Weber and El-Sayed [1987]	11/84 - 12/84	44	0 - 200	60 - 63	54 - 59	0.01 - 2.9	-
unpub. (KMS2)[a]	11/84 - 12/84	4	0 - 200	45 - 61	56 - 90	0.02 - 1.0	*5 - 42*
Cabrera et al. [1987]	1/85	15	0 - 31	62 - 64	58 - 64	0.19 - 16	12 - 201
Holm-Hansen et al. [1989]	1/85	10	0 - 75	64	64	0.10 - 30	-
Mullins and Priddle [1987] (JBS2)[a]	1/85 - 2/85	42	0 - 1750	60 - 65	54 - 67	<0.01 - 12	*5 - 310*
Uribe [1987] (ACS2)[a]	1/85 - 2/85	27	0 - 100	62 - 64	54 - 63	0.07 - 34	*17 - 872*
unpub. (BES2)[a]	1/85 - 2/85	46	0 - 150	60 - 64	54 - 67	0.01 - 38	-
Kottmeier and Sullivan [1987]	8/85 - 9/85	4	0 - 60	64	62 - 64	0.02 - 0.11	1 - 6
NASA data (Russia)[c]	12/85 - 3/89	21	0	60 - 62	55 - 57	0.13 - 1.2	-
Holm-Hansen and Mitchell [1991][b]	12/86 - 3/87	347	0 - 4378	62 - 64	60 - 63	0.01 - 25	13 - 175
Marino [1989]	1/87	26	4	59 - 63	51 - 62	0.50 - 5.1	-
Brightman and Smith [1989]	6/87	11	0 - 100	61 - 63	62 - 65	0.04 - 0.3	*4 - 11*
Figueiras et al. [1994]	12/88	18	0 - 150	60 - 61	47 - 54	0.10 - 3.4	*10 - 118*
Villafane et al. [1993]	1/91 - 3/91	50	0 - 750	60 - 62	53 - 59	<0.5 - 3.5	31 - 133[g]
Helbling et al. [1995]	1-3/90-93	260	0 - 750	60 - 62	53 - 59	0.40 - 6.3	5 - 330[g]
Mura et al. [1995]	1/93 - 2/93	44	0 - 25	62 - 65	63 - 57	0.06 - 4.5	-

[a] Data from the BIOMASS program (*Thorley and Trathan* [1994]). Cruise identifiers, in parentheses, indicate ship name and the BIOMASS campaign.

[b] RACER1 data.

[c] Data collected at Goddard Space Flight Center, National Aeronautics and Space Administration (NASA), (as cited in *Sullivan et al.* [1994]).

[d] Integrated over the euphotic zone; values in intalics integrated over 50 m.

[e] Mean monthly values are integrated over 200 m.

[f] Euphotic zone considered to be 0.1% surface light level.

[g] The authors integrated over 100 m; Data from *Villafane et al.* [1993] included in *Helbling et al.* [1995].

TABLE 2. Historical phytoplankton productivity data within the Palmer LTER region

Source	Date	No. Stations	Depth (m)	Latitude (deg S)	Longitude (deg W)	Hourly Production (mg C $m^{-3} h^{-1}$)	Int. Daily Production[a] (mg C $m^{-2} d^{-1}$)
El-Sayed et al. [1964]	3/63	15	0	55 - 64	58 - 66	0.6 - 18	-
Mandelli and Burkholder [1966]	2/65	35	0 - 50	61 - 65	57 - 66	-	210 - 1580
Bienati et al. [1977]	12/72 - 2/73	1	0 - 15	65 - 65	63 - 63	0.8 - 42	2460 - 3680[b]
Hapter and Wozniak [1983]	12/77 - 3/78	1	1 - 50	62 - 62	59 - 59	<0.01 - 6[c]	150 - 1500[d]
Hayes et al. [1984]	1/79	4	0	57 - 69	40 - 69	0.5 - 6	-
Schneider [1983]	12/80 - 2/81	42	0 - 100	55 - 64	50 - 64	<0.01 - 13[c]	19 - 1817
Tilzer et al. [1985]	11/80 - 12/80	23	0 - 100	55 - 64	54 - 64	<0.01 - 9	144 - 1459[e]
Bodungen et al. [1986]	11/80	6	0 - 55	62 - 63	55 - 58	<0.01 - 6[c]	233 - 1663[f]
Schnack et al. [1985]	12/80	4	0 - 60	61 - 63	55 - 62	<0.01 - 3	140 - 1120
Teixeira et al. [1986]	1/83 - 2/83	48	0 - 48	61 - 65	53 - 65	0.01 - 2	33 - 287[g]
Bodungen [1986]	11/83 - 12/83	9	0 - 58	62 - 64	55 - 62	0.05 - 6[c]	243 - 1562[f]
Weber and El-Sayed [1987]	11/84 - 12/84	11	0 - 60	60 - 63	55 - 59	0.2 - 4	585 - 2300[h]
Cabrera et al. [1987]	1/85	8	0 - 58	63 - 64	59 - 62	0.3 - 14	518 - 1939[i]
Kottmeier and Sullivan [1987]	8/85 - 9/85	4	0 - 60	64	62 - 64	<0.01 - 13[c]	11 - 1101
Holm-Hansen and Mitchell [1991]	12/86 - 3/87	347	0 - 80	62 - 64	60 - 63	-	70 - 3440
Brightman and Smith [1989]	6/87	9	0 - 50	61 - 63	62 - 65	-	3 - 11
Helbling et al. [1995]	1-3/90-93	206	0 - 750	60 - 62	53 - 59	-	50 - 930[j]

[a] Integrated production over the euphotic zone.

[b] Daily production rates were estimated from integrated hourly rates (122-180 mg C $m^{-2} h^{-1}$) by multiplying by the daylength. Productivity rates based on *in situ* incubations following *Steeman Nielsen* [1952]. Length and time of incubations not specified in paper.

[c] Hourly production rates estimated from daily rates by dividing by the daylength.

[d] Integrated over 50 m.

[e] Daily production rates were estimated from integrated hourly rates (9-79 mg C $m^{-2} h^{-1}$) by multiplying by the daylength. Productivity rates based on 6-hour simulated *in situ* incubations from 13:30-19:30.

[f] Euphotic zone considered to be 0.1% surface light level.

[g] Daily production rates were estimated from integrated hourly rates (2-15 mg C $m^{-2} h^{-1}$) by multiplying by the daylength. Productivity rates based on 4-hour simulated *in situ* incubations under white-cool fluorescent lamps.

[h] Productivity rates were based on 4-hour simulated *in situ* incubations centered around local noon. Daily productivity rates were estimated from integrated hourly rates (57-223 mg C $m^{-2} h^{-1}$) for 2 stations by multiplying by 10.4 hours (this includes the 4 incubation hours and assumes that the remainder of the day is equivalent to 6.4 noon-time hours).

[i] Daily production rates were estimated from hourly rates (26-99 mg C $m^{-2} h^{-1}$) by multiplying by the daylength. Productivity rates based on 8- to 10-hour simulated *in situ* incubations.

[j] Based on mean rates of production by cruise.

TABLE 3. Integrated average (and standard deviation from the mean[a]) phytoplankton productivity, biomass, and production per unit chlorophyll by month throughout the growing season, for the Palmer LTER region

Month	Integrated Avg. Productivity (mg C m^{-2} h^{-1})	Integrated Avg. Chlorophyll-a (mg chl-a m^{-2})	Production per unit Chlorophyll-a (mg C mg chl-a^{-1} h^{-1})
November	44 (38)	218 (143)	0.2 (0.3)
December	73 (83)	223 (159)	0.3 (0.5)
January	89 (108)	151 (196)	0.6 (0.5)
February	47 (51)	82 (104)	0.6 (0.5)

[a] Numbers in paranthesis are one standard deviation from the mean.

Because ancillary optical data (e.g., PAR vs. depth, depth of the euphotic zone, etc.) were not always available, we estimated integrated water column chlorophyll concentrations by taking 50 m as a representative euphotic depth and integrated all profiles to this depth (italicized values in last column of Table 1). We required vertical chlorophyll profiles selected for integration to have at least five data points over the 0-50 m interval and to have one value in the upper 5 m and one in the 40-50 m region. Comparison of data integrated to 50 m vs. integrated to the euphotic depth (results not shown) shows that the 50 m approximation underestimates integrated water column chlorophyll for clearest waters (< 0.1 mg chl-a m^{-3}) but is a good approximation for waters with higher concentrations of chl-a.

Historical phytoplankton productivity data (Table 2) are more limited and the methods more varied. All data reported here estimate productivity by the uptake of ^{14}C, but incubation methods included both *in situ* and simulated *in situ* (SIS) and incubation times varied from a few hours to full-day. Only data subsequent to the mid 1980's are considered "clean" [*Fitzwater et al.*, 1982]. The question of the reliability of historical phytoplankton productivity data, prior to the introduction of clean techniques, is of some concern. *Martin et al.* [1990] suggest that clean techniques are most important in open ocean oligotrophic regions where iron is limiting. In coastal waters, where iron is not considered to be limiting, clean techniques have less influence. Following this argument, we would expect little difference between "clean" and "classical" techniques for the historical data we present here for the shelf-slope waters west of the Antarctic Peninsula. Our method for converting hourly and daily rates for the various data sets is given in Table 2. Integrated water column productivity is obtained by integrating production over the depth of the euphotic zone or over 50 m if optical data was unavailable. Not all sets of data contained sufficient information for conversion to the standard units shown.

3.2. Chlorophyll Biomass

The highest recorded chl-a values shown in Table 1 are within the coastal ecosystem, on the order of 30-40 mg m^{-3}, and are reported to be associated with relatively episodic spring/summer blooms. Mean monthly vertical distributions of chl-a, based on shipboard observations, are shown in Figure 2*a*. Biomass accumulates from November to February with average concentrations of 5 mg m^{-3} and maximum values of 38 mg m^{-3} (Figure 2*a* and Table 1). From October to April average near surface chlorophyll is usually >1.0 mg m^{-3} and remains <1.0 from May to September. During the growth season (November to March), the chl-a concentration is relatively high to depths of about 100 m (usually >1.0 mg m^{-3}). The integrated chl-a over the euphotic zone ranges up to around 300 mg m^{-2} (Table 1). For the growth season from November through March, monthly integrated (over 50 m) chl-a historical data are summarized in Table 3. The large variances associated with these estimates are due to both temporal and spatial patchiness and the variability between inshore and offshore concentrations. The large variances also indicate the variable occurrence at any given locality of large blooms, with concentrations in the euphotic zone ranging up to 38 mg m^{-3}. A key question with respect to assessing the overall productivity of this coastal ecosystem is to quantify the space/time variability of what appears to be consistently reoccurring large phytoplankton blooms at this time of year. During winter there are few data, but the small number of stations sampled shows very low chlorophyll concentrations throughout the water column (<0.05 mg chl-a m^{-3}).

Inspection of the vertical distribution of chl-a (Figure 2*a*) shows that, on average, the maximum biomass is usually near the surface. Since these data are limited in both space and time, it is inappropriate to speculate on regional differences or hypothesize factors influencing seasonal variability. Most of the historical data are not only from late spring/early summer but are also from studies of short-term processes. Thus, these studies often targeted areas of high production and/or chlorophyll biomass, so that the estimates available are not necessarily representative of the whole area at any given time. This is in contrast to the LTER sampling strategy which aims to cover fixed and repeatable areas so as to obtain a representative sample from the west side of the Antarctic Peninsula.

Seasonal frequency distributions of chlorophyll maximum depth are shown in Figure 2*b*. Data were binned into depth categories from 0-5 m, 5-15 m, 15-25 m, etc. For those data that had vertical profiles with at least five data points (including one near the surface and one over 50 m), the maximum chlorophyll depth was determined and the frequency distribution plotted. The chlorophyll maxima were defined as a value

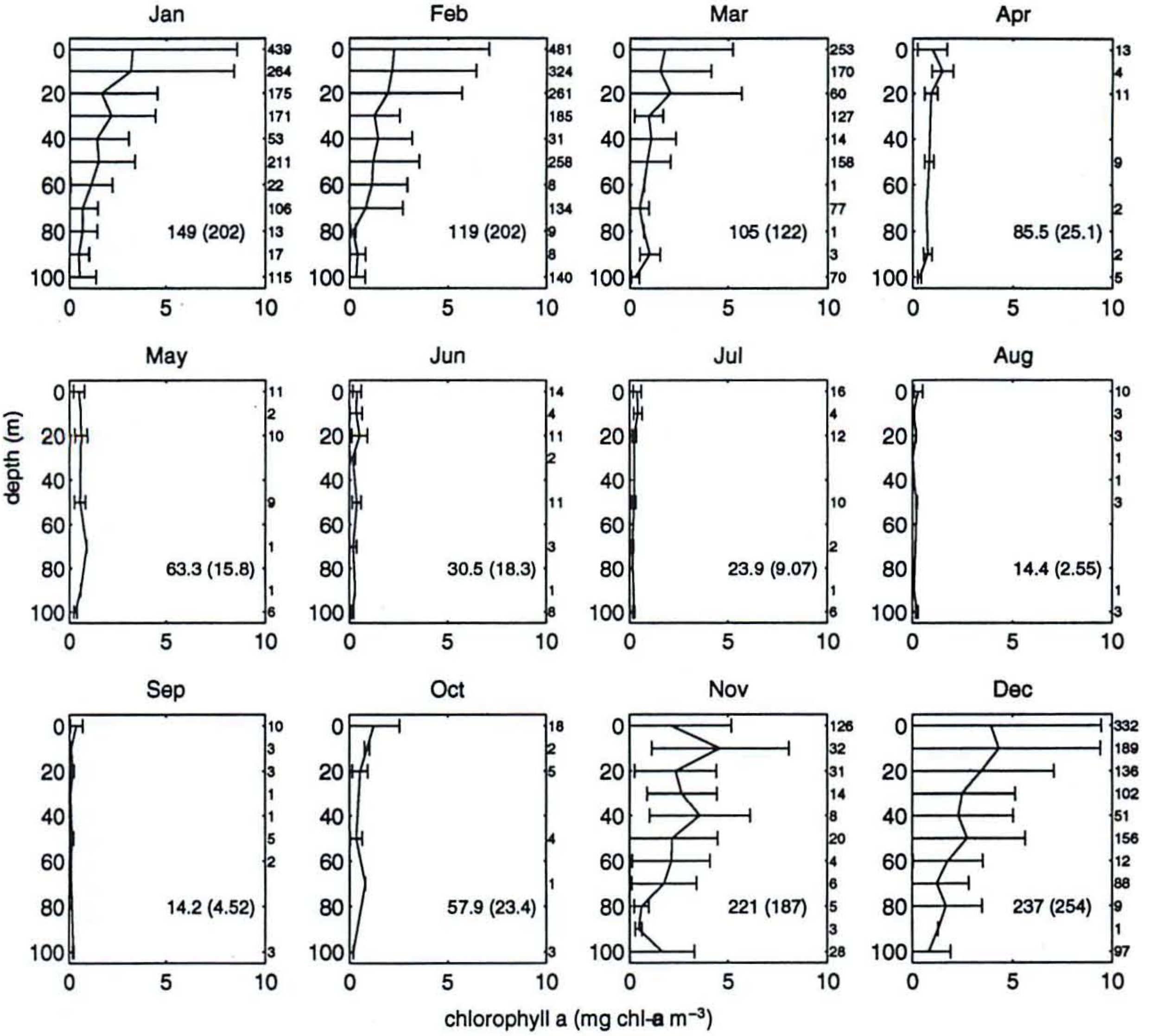

Fig. 2*a*. Monthly mean (solid line) and standard deviation (bars) profiles of chl-a concentrations (mg m^{-3}) versus depth (m) calculated for the historical data listed in Table 1. Numbers to the right of each monthly figure are the number of samples at each depth that were used to compute mean and standard deviation. Values shown in lower right of each figure are integrated values (mg chl-a m^{-2}) and standard deviations in parenthesis.

greater than 50% of the mean concentration for that station. From the available data, there does not seem to be significant seasonal variability in the depth structure of pigment biomass. About half the stations show maximum values in the top 15 m, with the rest of the stations showing subsurface chlorophyll maximum at depths of 16 m and deeper. These seasonal frequency distributions show that about half the time maximal biomass is in the mixed layer as suggested by numerous studies [*Burkholder and Mandelli*, 1965; *Mandelli and Burkholder*, 1966; *Biggs et al.*, 1982; *El-Sayed et al.*, 1983; *Holm-Hansen et al.*, 1989; *Mitchell and Holm-Hansen*, 1991b]. Although present through the year, deep chlorophyll maxima are more frequent in summer. The November and March profiles are similar with the hint of an apparent broad subsurface chlorophyll maximum around 10-20 m. This may be a result of the greater number of data points at surface (10-200) versus at subsurface (30-60) depths. If these profiles are representative of this CCSZ system, then pigment biomass is usually a near surface feature, with a suggestion of a seasonal cycle expressed as more subsurface chlorophyll later in summer.

For these waters there is a relatively tight coupling between surface chlorophyll and chlorophyll integrated to depth. This is verified by the linear relationship between chlorophyll at the surface and integrated to 50 m (Figure 2*c*). Consistent with earlier findings [*Comiso et al.*, 1990; *Holm-Hansen and Mitchell*, 1991], the data suggest that the surface waters in this area are good indicators of the phytoplankton biomass within the euphotic zone. Indeed, the value of the regression coefficients are similar to results presented for more temperate waters [*Smith and Baker*, 1978; *Brown et al.*, 1985]. When analyzed seasonally this relationship holds true for late spring, summer and fall but there are too few data to generalize for other times. This relationship is especially important with respect to remote sensing using ocean color satellite sensors (e.g., CZCS, SeaWiFS), where the upwelled signal comes primarily from the top attenuation length of the ocean.

Plate 1 is a contour plot of average summer surface chl-a from the historical data and averaged and plotted for the northern end of the LTER grid where sufficient data enabled contouring. These data show a strong on/offshore gradient in surface chlorophyll concentration. The range of average values spans over an order of magnitude going from greater than 10 mg m^{-3} nearshore to less than 1 mg m^{-3} further seaward on the shelf. On average, higher values are typically shoreward of the shelf break (500 m).

Figure 3*a* shows the mean monthly productivity data (mg C m^{-3} h^{-1}) vs. depth for the historical data listed in Table 2. Within this shelf-slope MIZ region daily phytoplankton productivity can reach very high values during spring and early summer. Column integrated production ranged from 2 to over 3000 mg C m^{-3} h^{-1}, the higher values comparable to those from the ocean's most highly productive areas. These high values are generally reported as episodic events limited in both space and time, however some studies indicate [*Holm-Hansen et al.*, 1989] that large phytoplankton blooms seem to be predictable from year to year and may be of widespread geographical significance. To date, estimation of aerial averages over time are speculative, requiring complementary time series and satellite coverage for increased accuracy.

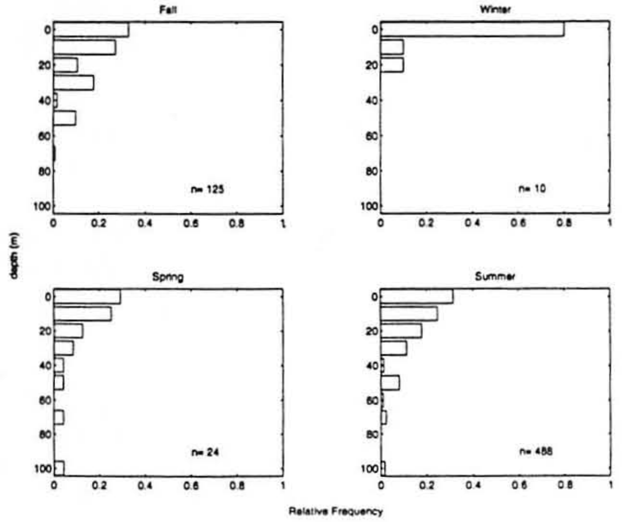

Fig. 2*b*. Seasonal mean frequency distribution of the depths of maximum chl-a concentrations based on the historical data listed in Table 1. Chlorophyll maxima are defined as values greater than 50% of the mean concentration for each vertical profile.

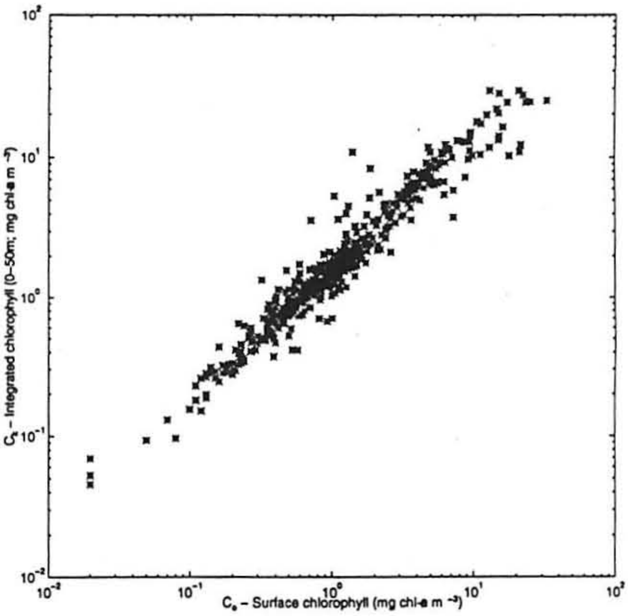

Fig. 2*c*. Relationship between surface chl-a concentration (C_o, mg m^{-3}) and water column chl-a integrated to 50 m and divided by the depth of integration (C_k, mg m^{-3}) for applicable historical data listed in Table 1. Regression equation is $\log(C_k) = 0.92 \log(C_o) + 0.05$, where $r^2 = 0.83$.

Figure 3*b* shows the productivity data normalized by chlorophyll biomass. The data are fewer because not all published productivity values included corresponding pigment biomass data and so only data for the four growth months are shown. These data are consistent with the hypothesis that production in the spring (Nov, Dec) occurs within relatively well mixed waters, whereas production in the summer (Jan, Feb) may be occurring during increased stratification and displaying light adaptation with increasing depth. Near surface values remain between 1 to 2 mg C (mg chl-a)$^{-1}$ h^{-1} throughout the growth season, well within the reported average for polar phytoplankton [*Platt et al.*, 1982].

Table 4 summarizes published historical photosynthesis vs. irradiance (P-I) parameters based on experiments carried out between 1965 and 1993. Data are mostly for spring and summer populations with the exception of one winter cruise in June 1987. Figures 3*c* and 3*d* show P^B_{max}, the maximum rate of photosynthesis per unit chl-a (assimilation number), and α, the initial slope of the P-I curve, for the historical data plotted as a function of percent incident PAR. P^B_{max} varies somewhat more than an order of magnitude, from 0.36 to 7.3 mg C (mg chl-a)$^{-1}$ h^{-1}, and the photosynthesis at limiting irradiance (α) shows a range of values spanning almost two orders of magnitude, from 0.002 to 0.11 mg C (mg chl-a)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$. Thus, P-I parameters for the Palmer LTER area are within the expected range based on polar temperatures and extrapolated from studies on temperate phytoplankton and are consistent with the range of data published for polar waters in general [*Smith and Sakshaug*, 1990]. There is no apparent depth dependence, in either P^B_{max} or α, for all the combined

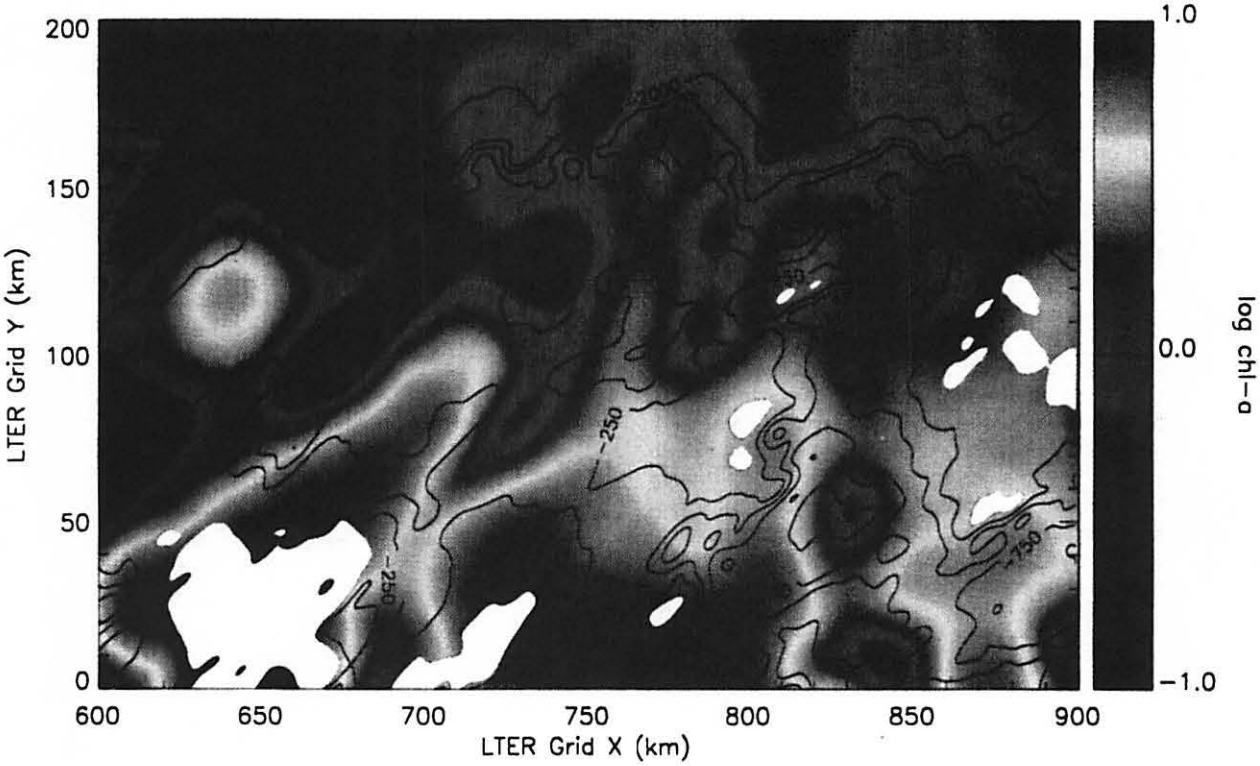

Plate 1. Surface chlorophyll concentration during summer (Dec, Jan, Feb) based on historical data listed in Table 1. Data averaged and contoured onto the LTER grid. Log chl-a in units of mg m^{-3}. Contours of bottom topography (depth in meters) also shown. White areas represent land.

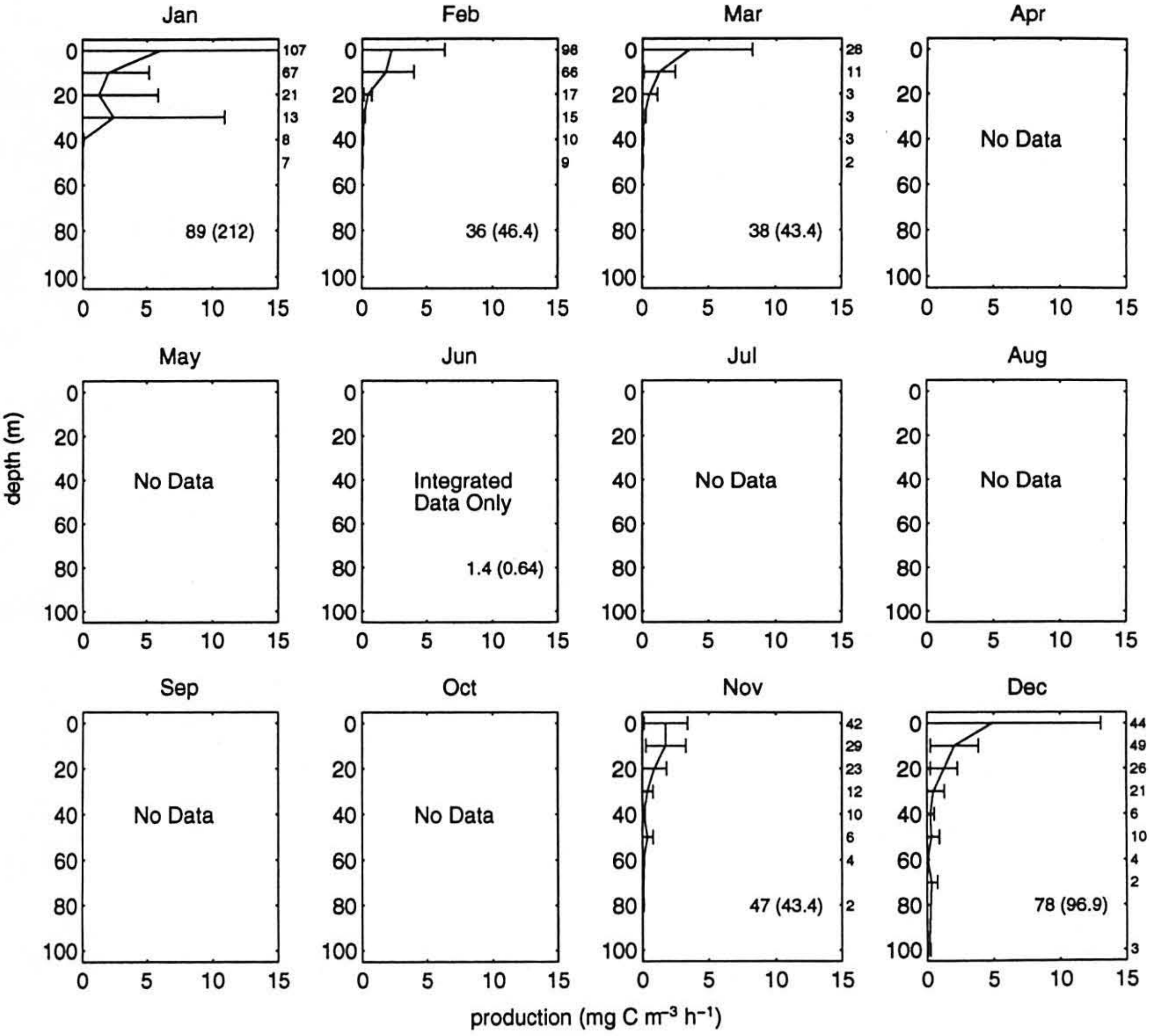

Fig. 3*a*. Monthly mean (solid line) and standard deviation (bars) profiles of phytoplankton productivity (mg C m^{-3} h^{-1}) versus depth (m) for the historical data listed in Table 2. Numbers to the right of each monthly figure are the number of samples at each depth that were used to compute mean and standard deviation. Values shown in lower right of each figure are integrated values (mg C m^{-2} h^{-1}) and standard deviations in parenthesis.

data. This could be due to a combination of factors, from the presence of a well mixed euphotic zone, to differences among stations and cruises which disguise differences due to species composition, etc. However, individual studies also did not find a clear depth dependence in these parameters [*Sakshaug and Holm-Hansen*, 1986; *Brightman and Smith*, 1989; *Figueiras et al*., 1994; *Helbling et al*., 1995]. The lack of an increase in α with depth for the data presented here suggests that there is no depth dependence for the average quantum yield which varies between 0.04 to 0.08 (mol C)/(mol PAR). *Sakshaug and Holm-Hansen* [1986] present data to show that $P^B{}_{\max}$ varies with the C/chl-a ratio and suggest, therefore, that the maximum carbon turnover rate is relatively independent of photoadaptation. This would seem to be an important characteristic of Antarctic algae in response to strong mixing and variable light regimes. The derived adaptation parameter, $I_k = P^B{}_{\max} / \alpha$, is somewhat less variable and generally lower than for temperate waters, suggesting to several authors that phytoplankton in these waters are adapted to low light. Several researchers [*Figueiras et al*., 1994; *Helbling et al*., 1995] found that I_k was close to the mean PAR value found in the mixed water column which suggest that Antarctic phytoplankton are well adapted to take advantage of the low light, high nutrient, well mixed environment.

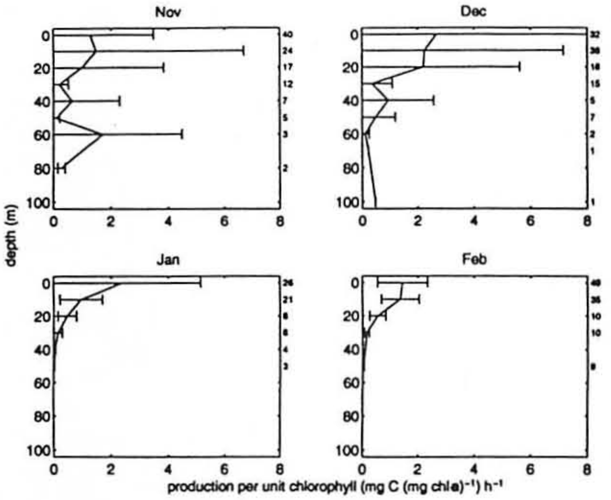

Fig. 3*b*. Monthly (Nov - Feb) mean values of production per unit chlorophyll (mg C (mg chl-a)$^{-1}$ h^{-1}) versus depth (m) based on historical data (Tables 1 and 2).

4. SATELLITE DATA

Composite images of surface chl-a concentrations for the Palmer LTER grid, estimated from historical Coastal Zone Color Scanner (CZCS) data [*Feldman et al.*, 1989] using a Southern Ocean pigment algorithm [*Sullivan et al.*, 1993], are shown in Plates 2 and 3. CZCS data were first combined into monthly averages by summing all available data for each 20 km x 20 km pixel for the life of the satellite (November 1978 to June 1986). The data were then further composited into four seasonal climatologies. Plate 2 shows the fall image of surface chl-a concentrations for the LTER sector and regions north to the Drake Passage. Plate 2 clearly illustrates the significantly higher pigment biomass between the shelf-slope waters west of the Peninsula and the lower biomass of more pelagic waters. Typically, the LTER area is relatively ice free by fall [*Stammerjohn and Smith*, this volume], and the relatively high pigment biomass in the lower left of Plate 2 may be indicative of the influence of the MIZ during this period. Alternatively, the higher biomass along 80°W could be associated with the southernmost major front of the Antarctic Circumpolar Current which has been shown to be associated with higher levels of productivity south of this front [*Read et al.*, 1995; *Boyd et al.*, 1995]. Plate 3 shows seasonal images for the LTER grid only. In this figure there are no data for the top panel during (austral) winter. The 2nd panel shows the spring chl-a average concentrations with high values in the northeast (bottom right) corner of the grid. The remainder of the grid may have been ice and/or cloud covered and consequently show no data. The 3rd and 4th panels show summer and fall chl-a average concentrations, respectively. Satellite coverage of this area is incomplete, so these data are primarily suggestive of *regional scale* variability and are not necessarily an accurate representation of *true seasonal* variability. However,

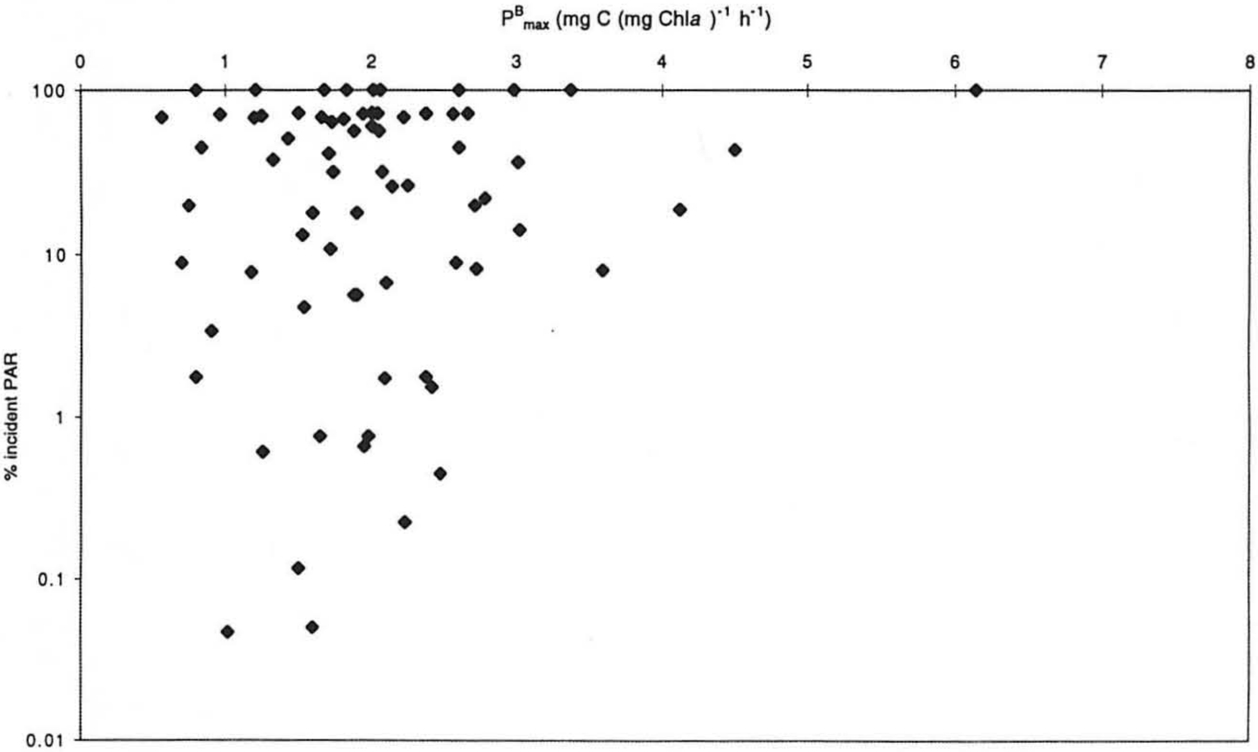

Fig. 3*c*. Maximum photosynthesis per pigment biomass (P^{B}_{max}, mg C (mg chl-a)$^{-1}$ h^{-1}) vs. depth (m) expressed as % Photosynthetic Available Radiation (PAR) based on historical P-I data listed in Table 4.

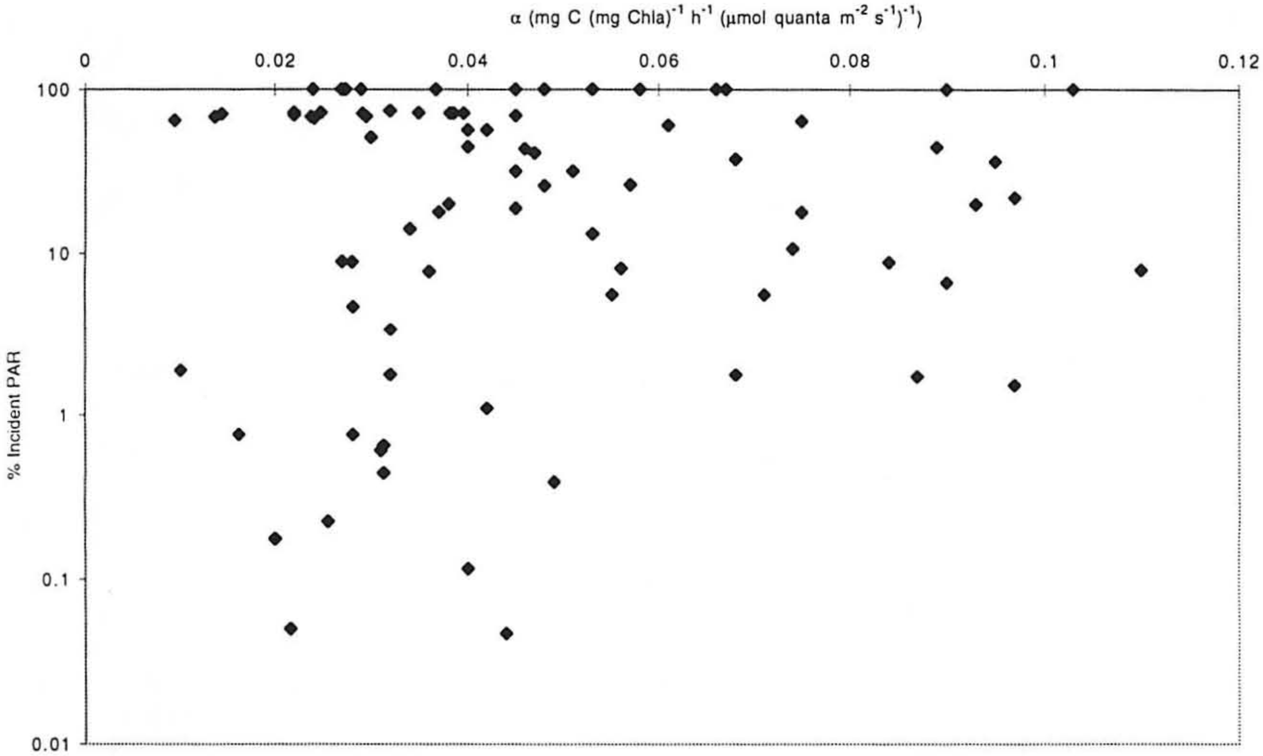

Fig. 3*d*. Initial slope of P-I curves (α, mg C (mg chl-a)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$) vs. depth expressed as % incident PAR based on data listed in Table 4.

images shown in Plate 3 are consistent with the hypothesis of a seasonal trend from north-east to south-west (right to left on Plate 3) which follows the retreating sea ice. An important caveat is that we do not know what bias, if any, is caused by use of only clear sky data used for the composite images [*Michaelsen et al.*, 1988]. We do know that these satellite data are generally consistent with ship observations, because historical chlorophyll data were used to develop the Southern Ocean pigment algorithm [*Sullivan et al.*, 1993]. Also, the overall similarity between Plates 1 and 3 suggests that Plate 3 is an accurate regional representation of spatial variability in surface chl-a.

5. DISCUSSION

Both the historical pigment biomass and phytoplankton productivity data in addition to the average, composite ocean color satellite imagery clearly suggest and illustrate that the shelf-slope system west of the Antarctic Peninsula is fundamentally different from the pelagic areas of the Antarctic marine ecosystem. The Palmer LTER area is a complex combination of two distinctive subdivisions [*Treguer and Jacques*, 1992], the coastal and continental shelf zone (CCSZ) and the seasonal ice zone (SIZ). This coastal component of the Antarctic marine ecosystem is: (1) annually swept by sea ice; (2) influenced by meltwater from glaciers and icebergs; (3) inclusive of areas providing some protection from wind and storms; (4) potentially enriched by essential micronutrients from land; (5) supportive of massive blooms that do, in fact, reduce macronutrients; and (6) supports phytoplankton biomass and productivity levels at least a factor of two and perhaps as much as a factor of ten higher than the open ocean zone (OOZ). While the surface area of this coastal ecosystem is relatively small, the annual space/time integral of major phytoplankton blooms is significant. In particular, the pulsing of these blooms, tied to sea ice habitats [*Smetacek et al.*, 1990; *Ross and Quetin*, 1991] are likely to be especially significant for the trophic dynamics of the ecosystem.

The on/offshore gradient is consistent with the blue/green ocean dichotomy [*Berger et al.*, 1989] of the rest of the world's oceans where there are two pathways for the transfer of organic carbon from near surface photosynthesis to burial in the sediment, one for pelagic conditions and one for neritic conditions. It may also be associated with a trace micronutrient, like iron, but this has yet to be tested. Further, it is consistent with estimates of new production for pelagic and marginal ice zone (MIZ) areas of the Southern Ocean, where the f-ratio is a factor of four higher for the MIZ [*Smith*, 1991]. The f-ratio, the ratio of nitrate uptake to total nitrogen uptake [*Eppley and Peterson*, 1979] is used as a measure of new production available for export. This has been reviewed for polar phytoplankton [*Smith and Sakshaug*, 1990] and the f-ratio found to span the same range as for other oceanic waters. Areas with high productivity tend to have high f-ratios, implying that these areas have a sufficient nutrient supply, but also that there must be mechanisms for resupply of these nutrients on an annual basis. Consequently, this coastal area west of the Antarctic Peninsula is a likely site for significant new production and

TABLE 4. Historical Photosynthesis-Irradiance (PI) parameters[a] within the Palmer LTER region

Source	Date	α	β	P^B_{max}	I_k'	ϕ
Burkholder and Mandelli [1965]	2/65	-	-	0.70 - 5.40	-	-
Tilzer et al. [1985]	11/80	0.002 - 0.040[b]	-	0.36 - 1.19	19 - 175	0.002 - 0.034
Tilzer et al. [1986]	10-11/83	0.014 - 0.040[b]	-	0.56 - 2.66	44 - 95	0.012 - 0.034
Sakshaug and Holm-Hansen [1986]	3/84	0.009 - 0.049	-	0.75 - 4.40	38 - 190[c]	0.008 - 0.042
Cabrera and Montecino [1990]	1/85	0.018 - 0.084	-	1.00 - 7.30	54 - 87	0.015 - 0.072
Holm-Hansen and Mitchell [1991]	12/86-3/87	0.06[d]	-	1.1[d]	18[d]	0.051
Brightman and Smith [1989]	6/87	0.006 - 0.066	0.01 - 8.52	0.22 - 2.44	34 - 177	0.005 - 0.057
Figueiras et al. [1994]	12/88	0.024 - 0.110	0.03 - 6.00	0.70 - 4.78	20 - 84	0.021 - 0.094
Helbling et al. [1995]	1-3/90-93	0.013 - 0.029[d]	-	1.02 - 2.92[d]	91 - 111[d]	0.011 - 0.025

[a] alpha (α) = initial slope of P-I curves, mg C (mg chl-**a**)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$;

beta (β) = index of photoinhibition, mg C 10^{-3} (mg chl-**a**)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$;

P^B_{max} = light-saturated chl-**a**-specific rate of photosynthesis, mg C (mg chl-**a**)$^{-1}$ h^{-1};

I_k = saturation parameter for P-I curves, μmol quanta m^{-2} s^{-1};

phi (ϕ) = quantum yield, mol C (mol PAR)$^{-1}$ (computed from α, with k_c= 0.027 m^2(mg chl-**a**)$^{-1}$ following *Kirk* [1983]; *Tilzer et al.* [1985]).

[b] Units converted to above by multiplying by 3.6 s h^{-1} mmol μmol^{-1}.

[c] Calculated by taking P^B_{max}/α.

[d] Authors calculated values by taking the photosynthetic assimilation numbers from all stations as a function of the mean irradiance to which the samples were exposed during the incubation periods.

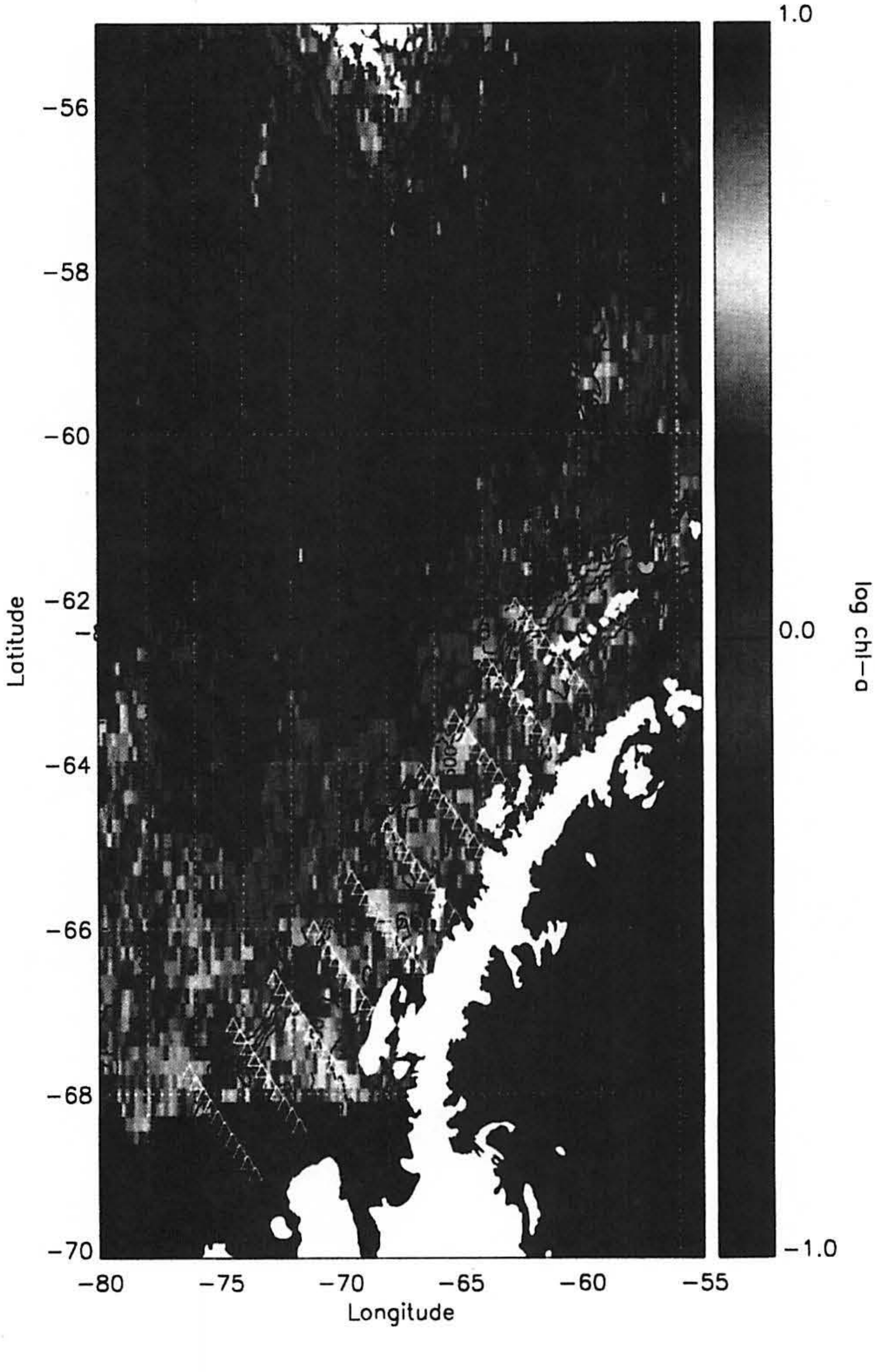

Plate 2. Surface chlorophyll concentrations (log mg chl-a m^{-3}) as estimated from historic (Nov 1978 to June 1986) Coastal Zone Color Scanner data. Composite image for fall (March, April, May) with the Antarctic Peninsula at lower right and tip of South America top middle (land in white). Light triangles indicate the Palmer LTER cardinal stations and dark lines show bottom topography (depth in meters).

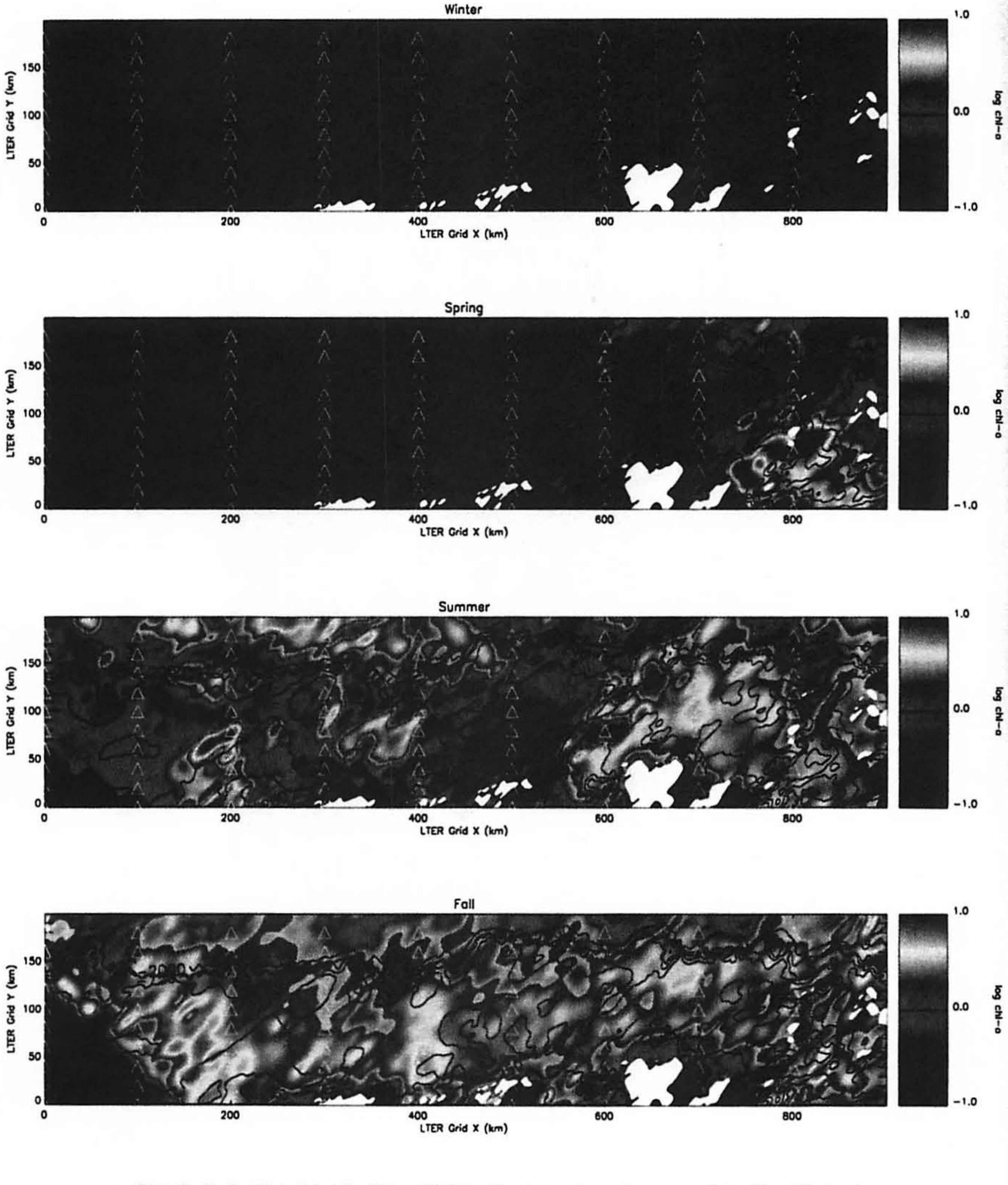

Plate 3. As for Plate 2, but for Palmer LTER grid only and for each season: winter (Jun, Jul, Aug), spring (Sep, Oct, Nov), summer (Dec, Jan, Feb), and fall (Mar, Apr, May). White areas represent land.

removal of carbon flux from the surface layer, even though mechanistic details remain unknown.

If the average values for integrated productivity (Table 3) are reasonably representative of the Palmer LTER region, then the average primary production of this CCSZ area is of the order of a few hundred g C m^{-2} y^{-1}, which, while lower, is comparable to other productive coastal areas of the world's oceans [*Chavez and Barber,* 1987]. This CCSZ, which is coupled to the OOZ which maintains a low but apparently consistent biomass (on the order of 0.1 mg chl-a m^{-3}), is obviously adequate to support high biomass levels of birds and mammals. Key questions of this Antarctic coastal ecosystem may concern mechanisms coupling the OOZ to the CCSZ and SIZ in the maintenance of relatively high biomass in higher trophic levels.

It is unlikely that any single factor controls production in these waters. Indeed, complexity and opportunism may govern the response with which various factors alternate in importance under pronounced environmental variability. Temperature exerts a physiological pressure, perhaps setting an upper limit to algal growth, but is not dominant. Light, an essential driving factor, is modulated not only by variability in incident irradiance but also by physical factors such as water column stability and the presence or absence of sea ice. Thus, even though Antarctic phytoplankton seem to be adapted to low light, the availability and utilization of light depends upon environmental factors and habitat light history. A confounding anthropogenic influence is the potential for increased ozone related UVB and its impact on phytoplankton communities. In addition, if massive phytoplankton blooms are periodic and geographically widespread within this area [*Holm-Hansen et al.*, 1989], with corresponding drawdown of nutrients, then nutrient limitation may be more important than currently supposed. To the extent that massive blooms are a significant component of the shelf ecosystem, a key question becomes one of understanding bloom dynamics, regulation and, in particular, mechanisms that terminate blooms. Trace metal limitation is thought to be unlikely in coastal regions but few data exist to support this assumption and the persistent on/offshore gradient in biomass suggests a mechanism linked to the proximity of the coast for higher biomass accumulation. There is evidence that predator-prey cycles can be rapid, and the role of grazing, in particular grazing linked to seasonal development between krill and phytoplankton, remains a critical and outstanding question.

Episodic events and massive phytoplankton blooms characterize the very foundation of the Southern Ocean food web. To date, spatial and temporal estimates of pigment biomass and phytoplankton production are constrained by limited and aliased data. Complementary studies of seasonal and interannual variability of phytoplankton, coupled with spatial satellite coverage, as planned for the Palmer LTER program, hold promise of increased accuracy of the estimates of phytoplankton biomass and production.

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